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The Morphology of *Eodiscoglossus*, A Complete Jurassic Frog

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INTRODUCTION

Almost perfectly preserved specimens of anurans from the Mesozoic are rare and merit thorough study. The frog described in the present paper was collected in the middle 1940's by L. Ferrer-Condal at the famous locality of Monsech, near the village of Rubies, Province of Lérida, Spain. This locality is renowned for its beautifully preserved fishes, invertebrates (insects and crustaceans), and reptiles (including two genera of lizards; Hoffstetter, 1966). It has also yielded another frog, *Monsechobatrachus*, but the specimen is poorly preserved (Hecht, 1963).

The anuran specimen described here includes both a part and a counterpart. The more complete portion, the part, is in the Museum of Science in Madrid, and the counterpart is in the private collection of Ferrer-Condal. The part was figured in Piveteau (1955); the same photograph appeared in Meléndez (1957) under the name of *Eodiscoglossus santonjæ* Villalta. Although a brief summary of its features was listed by Hecht (1963), until now no detailed study of *Eodiscoglossus* has been published. In order to evaluate its phylogenetic significance, a complete description of this specimen is necessary.

The fossil material from Monsech fluoresces extremely well in ultraviolet radiation (3660 Å). Fluorescence photographs made by the meth-

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ods described in Hecht (1960), Colbert and Tarka (1960), and Rolfe (1964) show more detail than can be observed directly in incandescent light. All the photographs for the present paper show the specimen under black light.

ACKNOWLEDGMENTS

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TAXONOMY

CLASS AMPHIBIA

SUPERORDER SALIENTIA

ORDER ANURA

FAMILY DISCOGLOSSIDAE

EODISCOGLOSSUS VILLALTA, 1957

TYPE SPECIES: *Eodiscoglossus santonjae* Villalta.

DISTRIBUTION: Santa María de Meyá Formation, Upper Jurassic (Upper Kimmeridgian); Province of Lérida, Spain.

REVISED GENERIC DIAGNOSIS: A small discoglossid frog characterized by its toothless upper jaw, five digits on the forelimb, nuptial pad on the first digit with accessory nuptial pads on the second and third digits, and the presence of a plectrum. It is distinguished from all discoglossid frogs by its toothless maxilla and premaxilla; from the fossil *Scotiophryne*, *Latoria* and *Zaphrissa* by the lack of cranial ornamentation; from *Bombina* by the presence of a plectrum; and from all other living forms by its smaller size and secondary sexual ornamentation of the male.

Eodiscoglossus santonjae Villalta, 1957

TYPE: Unnumbered specimen, Museum of Science, Madrid, Spain.

HORIZON AND LOCALITY: Upper Kimmeridgian¹ of the Santa María de Meyá Formation, Province of Lérida, Spain. The quarry from which the specimen comes is in the vicinity of the village of Rubies, about 30 kilometers north of Balaguer.

SPECIFIC DIAGNOSIS: Same as for the genus.

DESCRIPTION: The skeleton is divided between the part and the coun-

¹ Krusat (MS.) stated that the main quarry of this deposit is of Upper Portlandian age.

terpart. The part (fig. 1) is composed of an almost complete skull, vertebral column, pectoral girdle, right forelimb and right hind limb, a less complete left forelimb, an incomplete pelvic girdle, and a short piece of the femur of the left hind limb. The outline of the general body shape is clearly seen. Pigment probably representing the retina is indicated, and dark areas are also present in the region of the abdomen. Most of the heavily keratinized parts of the body are preserved, as, for example, the nuptial pads on the first three digits of the forelimb.

The counterpart (fig. 2), which is less complete, includes fragments of the skull, parts of the vertebral column, part of the right forelimb and pelvic girdle, and most of the right hind limb.

MEASUREMENTS: Measurements are best determined from the part. The specimen measures 27.3 mm. from the premaxilla to the ischium. The skull length, from the premaxilla to the occipital condyles, is about 7.5 mm. The width of the skull across the quadratic-squamosal area is 5.0 mm. Approximate lengths are given for the following: Humerus, 6.0 mm.; urostyle, 9.0 mm.; femur, 12.4 mm.

SKULL: The rounded outline of the skull (figs. 3 and 4) is broken anteriorly by the tusklike projections of the premaxillae that extend anterolaterally. These processes probably represent the crushed dorsal processes of the premaxillae. A small, rounded body on the postero-exterior border of each premaxilla may be the laterally displaced olfactory capsule. Directly posterior to the clearly demarcated limits of the premaxillae lie the crushed, but apparently paired, nasal bones. Behind the nasals, there is a small yellowish area that may represent cartilage. Under black light it appears (fig. 3) as an area of greater fluorescence, and it may represent the dorsal portion of the sphenethmoid. Behind this is the badly crushed frontoparietal, preserved as the outline of an impression and lacking the left anterior portion. It most probably has a median fontanelle. Its posterior boundaries are not clear. A crushed supraoccipital abuts against the frontoparietal. Its posterior border has been pressed against the exoccipitals so that the occipital condyles have been displaced laterally (fig. 3).

Badly crushed prootics lie lateral to the posterior border of the frontoparietal and the exoccipital. They differ slightly in color from the surrounding bone, but the features are not distinct. On the posterior border of the left prootic there is a definite barlike bone (fig. 3), slightly widened on the internal border. It is most probably the plectrum of the columella (Eiselt, 1944; Barry, 1956). Slightly more displaced, but in a similar position on the right side, is the other plectrum.

As preserved, the right and left mandibles (figs. 3 and 4) lie internal

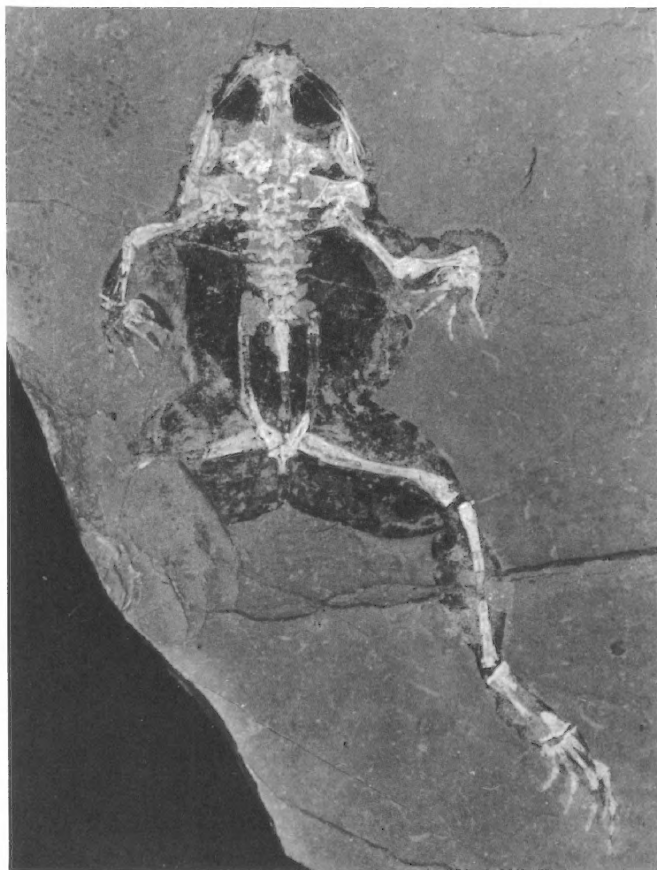


FIG. 1. *Eodiscoglossus santoniae* Villalta. Part, photographed under black light. $\times 2.25$.

to the upper jar margin. On the right side, the anterior portion of the mandible passes over the pigmented area of the orbit. It is complete, with the dorsal articulating surface visible. The left mandible is also complete except for its anterior tip. There is no indication of teeth on the lower jaw.

Both right and left maxillae are split through their longitudinal axes (fig. 3). Although the sutures are not visible between the posterior portions of the mandible (fig. 4), it is probable that the quadratojugal is present. The longitudinal split in the maxillae prevents observation of the maxillary margin, but the complete absence of displaced teeth suggests an edentulous condition. The squamosals are crushed flat between the prootics and the posterior borders of the mandibles (fig. 3). They are

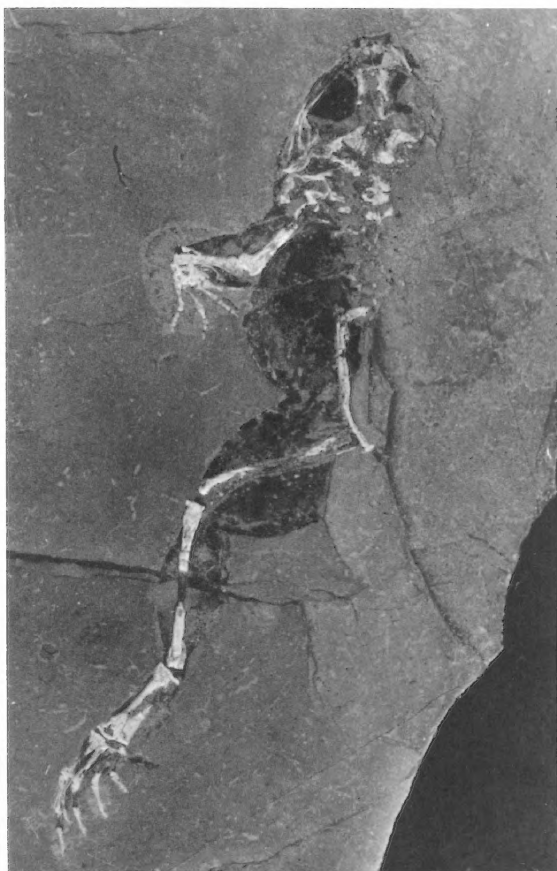


FIG. 2. *Eodiscoglossus santonjae* Villalta. Counterpart, photographed under black light. $\times 2.25$.

probably T-shaped. The pterygoids are visible beneath the squamosals on either side.

VERTEBRAL COLUMN: There are eight presacral vertebrae (fig. 8). The first seven are represented by crushed neural arches that bear low neural spines. In the area of the vertebral column there is a light gray matrix. This contrasts with the black pigmented areas that may represent skin or other tissues. The eighth vertebra is represented by a bone-filled depression. The sacrum and a portion of the urostyle are also preserved.

The first vertebra, or atlas, is badly crushed, but a low neural spine is evident. The condylar facet can be seen on the right side, and directly anterior to it is a remnant of the right occipital condyle.

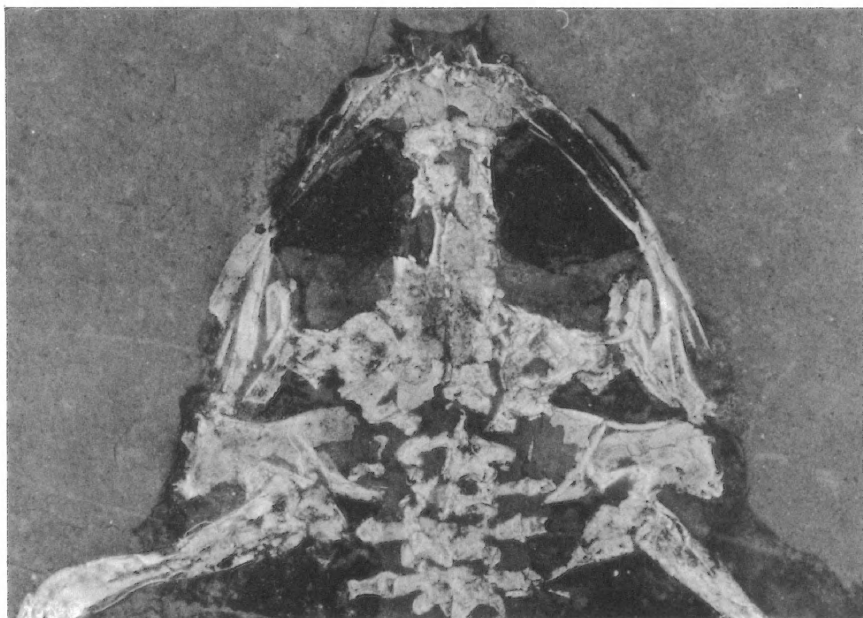


FIG. 3. Skull and pectoral girdle of *Eodiscoglossus santoniae* Villalta photographed under black light. Part. $\times 4.5$.

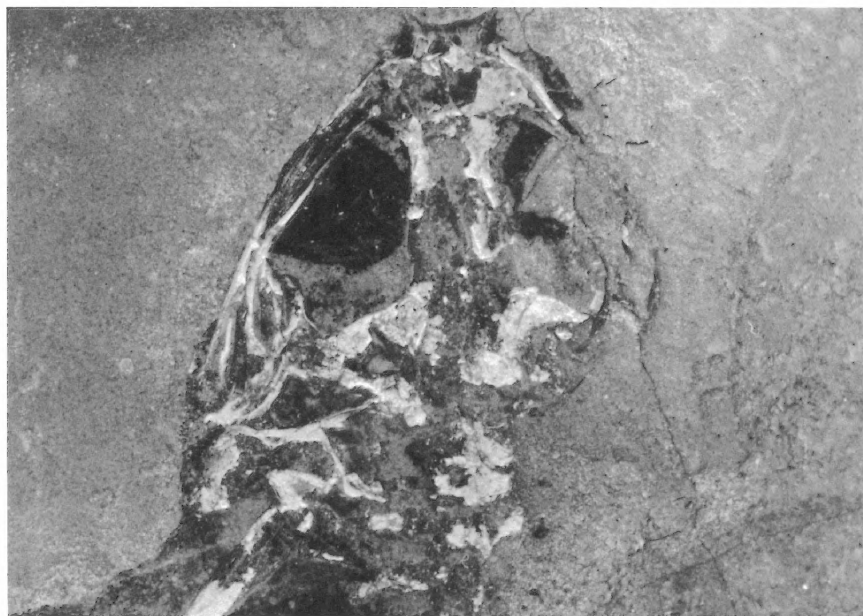


FIG. 4. Skull and part of pectoral girdle of *Eodiscoglossus santoniae* Villalta photographed under black light. Counterpart. $\times 4.5$.

The second vertebra also has an almost complete neural arch with an anteriorly placed transverse process. The right transverse process bears an articulating rib.

The third vertebra is similar to the second, but it is more complete. Its neural spine appears to be thick and low. The neural arch is longer and heavier than that of the anterior vertebrae. The right transverse process bears an articulating rib. The left transverse process is also well developed, but the articulation with the rib is not clear. Both the transverse process and rib overlie a portion of what is probably the left coracoid. The postzygapophyseal-prezygapophyseal contact with the posterior vertebra is well preserved.

The well-preserved fourth vertebra is similar to the three preceding ones. Its neural arch is crushed and the neural spine obscure. The transverse processes are wide; the left one clearly bears a rib. On the right side the transverse process and rib overlie the internal end of the clavicle.

The transverse processes on the fifth vertebra are narrow, and they do not bear any ribs. They are directed laterally in a manner similar to the more anterior vertebrae.

The sixth vertebra appears to be shorter than the preceding one. Its neural spine is not clearly preserved and its transverse processes, which are thin and short, are directed slightly forward.

The seventh vertebra is completely crushed. It bears, on the left side, a distinct anteriorly projecting, thin transverse process. The eighth vertebra is represented by remnants of bone only. A sliver of bone on the left side probably represents the transverse process. This was directed anteriorly, as indicated by both the sliver and a shallow impression. A similar anteriorly projected depression represents the right side.

The ninth vertebra (figs. 6 and 7), or sacrum, is indicated by a bone-line depression. A proximal fragment of the simple diapophysis extends in the direction of the ilium on the right side. Its continuations to the ilium is represented by a black pigmented imprint. On the left side of the sacrum there is a short stub and an impression representing the sacral diapophysis. To the left of the sacrum is a gray hatchet-shaped area resembling an expanded sacral hypophysis. This is in contact with the anterior end of the ilium. However, figures 2 and 7 clearly demonstrate that the sacral diapophyses are not expanded.

UROSTYLE: Only the crushed anterior portion of the urostyle (figs. 8 and 9) is preserved. It is not possible to determine with certainty whether it has a single or double condyle for articulation with the sacrum. The evidence suggests a single condyle. The presence of a transverse process on the anterior portion of the urostyle, the usual condition in the Disco-

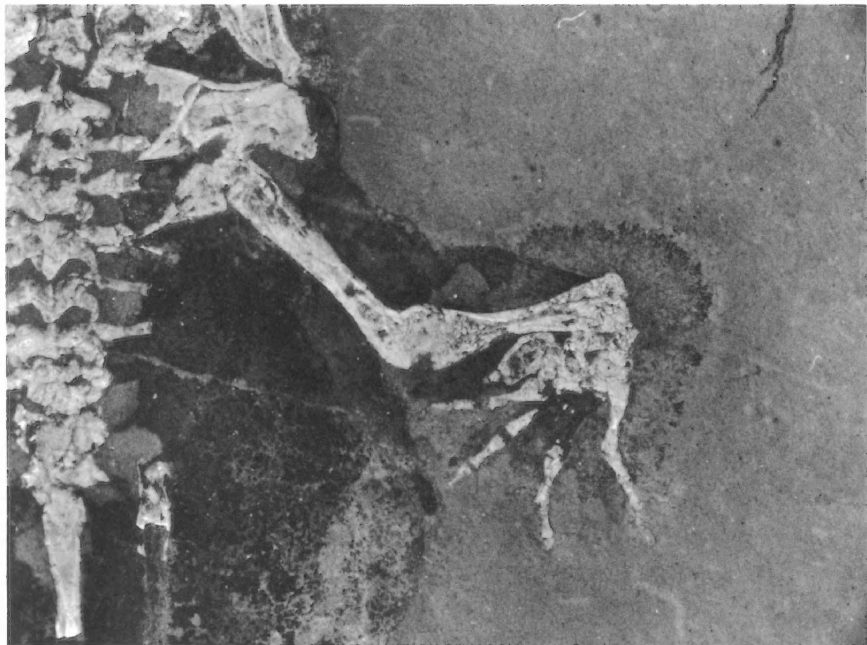


FIG. 5. Vertebral column, right pectoral girdle, right forelimb of *Eodiscoglossus santonjae* Villalta photographed under black light. Part. $\times 4.5$.

glossidae, is not indicated. The urostyle is represented posteriorly by an impression in the matrix that extends to the pelvic symphysis. The urostyle is surrounded by black pigment that covers all the area between the anteriorly projecting arms of the ilia. Anteriorly on the left side of the urostyle there is a gap in the approximate region occupied by the transverse process in other discoglossids. On the right side there is a more limited gray area, again in the appropriate region for the transverse process. However, there is no indication of bone, and therefore no conclusive evidence for the transverse processes.

PECTORAL GIRDLE AND LIMBS: The pectoral girdle and limbs (figs. 5, 6, 7, and 8) are preserved on both the right and left side, including the suprascapula, scapula, coracoid, humerus, radio-ulna, carpus, metacarpus and digits, but there are only indistinct remains of the clavicle. The entire pectoral girdle lies within the pigmented area of the body outline.

The details of the scapula are obscured by the overlying suprascapula. The latter appears to be a broad thin bone, as it is in all frogs. On the left side, the internal, or dorsal, process of the suprascapula points internally

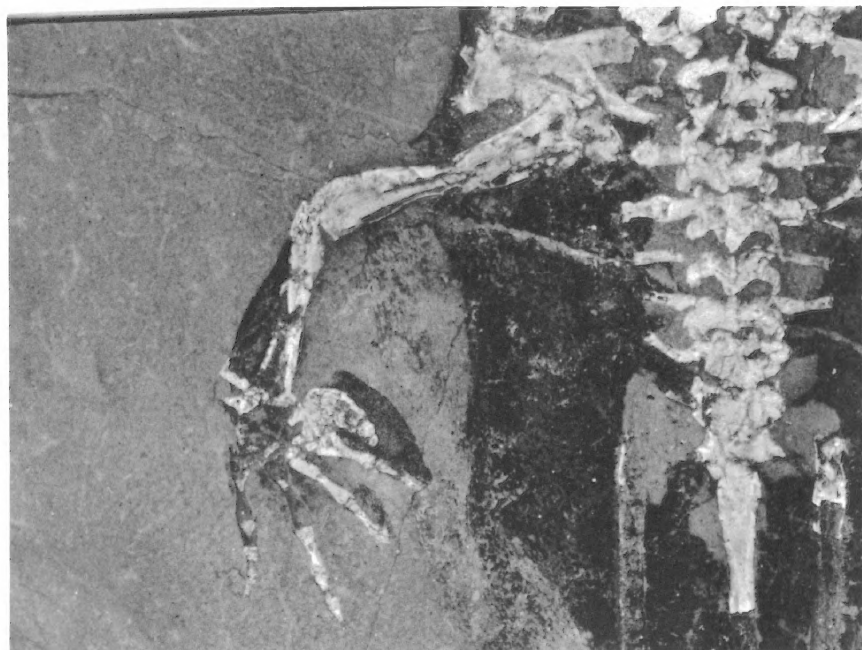


FIG. 6. Vertebral column, left pectoral girdle, left forelimb of *Eodiscoglossus santoniae* Villalta photographed under black light. Part. $\times 4.5$.

toward the vertebral column (fig. 6). The various processes of the scapula are not clearly visible, but on the right side there are indications of a pars glenoidalis and central foramen (Proctor, 1921). On the right side, posterior to the scapula but in contact with the head of the humerus, is the external half of the coracoid (fig. 5). The distal portion of the coracoid is swollen, and the proximal portion has a narrow neck. On the left side (fig. 6), a thin sliver of bone extends from a position anterior to the transverse process of the third vertebra under the thin portion of the blade of the suprascapula. This curved bone is probably the clavicle. Posterior to it is a pigmented depression that may represent the external inflated portion of the coracoid.

Both humeri are in approximately normal positions in relation to the shoulder girdle. The right humerus (fig. 5), which is crushed flat, is a long cylindrical bone bearing a distinct condyle at its distal end. A slightly enlarged process, outlined only in lateral view, is probably the ectepicondyle. The ball of the humerus abuts against the well-preserved radio-ulna. The radio-ulna bears a short olecranon process and distinct sulcus longitudinalis (Bolkay, 1919). The distal portion of the radio-ulna shows

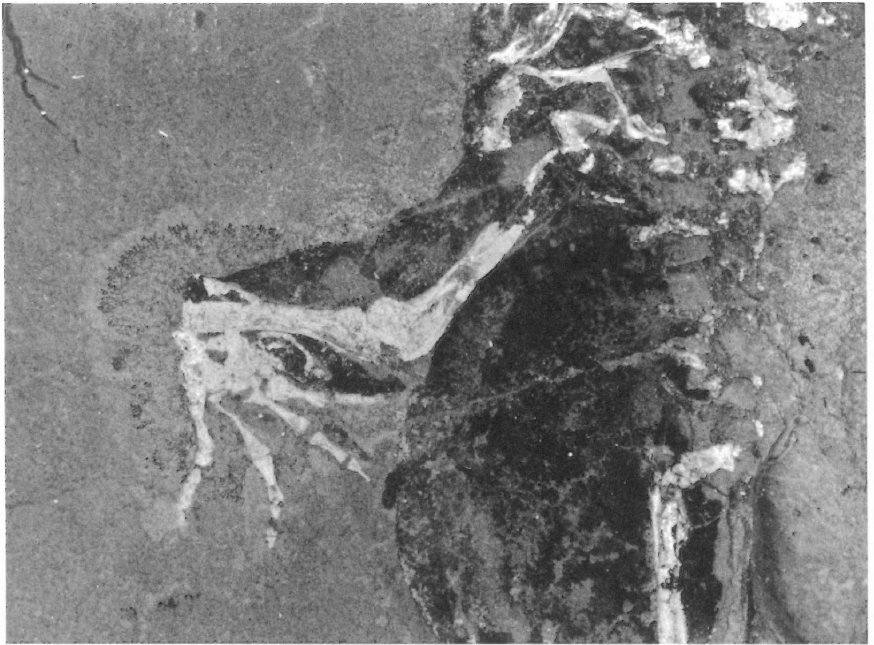


FIG. 7. Vertebral column, right pectoral girdle, right forelimb of *Eodiscoglossus santoniae* Villalta photographed under black light. Counterpart. $\times 4.5$.

a whitish area that probably represents the calcified cartilaginous cap. On the left side the humerus (fig. 6) is crushed showing the posterior aspect. The humerus articulates with an incompletely preserved radio-ulna. Part of the latter is preserved as an imprint. The distal portion is represented by a thin sliver of what is most probably calcified cartilage.

The right carpus (figs. 5 and 7) has been split between the part and counterpart of the specimen. A comparison reveals that there are at least four large carpals present making up the proximal and central series. This carpal pattern compares favorably with the characteristic discoglossid pattern figured by Howes and Ridewood (1888). On the left side only the most proximal portion of the proximal carpals are represented, but the imprints of the remaining ones are clear.

There is an enlarged darkened area surrounding the pollex of both right and left hands (figs. 5 and 6). The first digit, or pollex, is supported by a swollen metacarpal. It presumably had a complex shape, as its surface is marked by minute cavities. The proximal phalanx of the first digit is also enlarged and triangular in shape. The two distal phalanges are small nubbins. Under high magnification the black imprint sur-



FIG. 8. Vertebral column, posterior portion of skull of *Eodiscoglossus santonjae* Villalta photographed under black light. Part. $\times 4.5$.

rounding the digit reveals a roughened surface, suggesting that it was originally covered by minute papillae. The impression resembles that of keratinized tissue often found in living frogs. The imprint extends beyond the first digit and seems to attach itself along the full length of the second digit. Although both the left and right hands have been preserved in different positions, the keratinized areas seem to show the same relationship between the pollex and the second digit.

The second metacarpal and the two phalanges of the second digit are complete. The keratinized thumb area follows closely the outline of the bones of the second digit. The proximal phalanx is slightly less than half the length of the metacarpal. The distal phalanx is about one-quarter the length of the proximal phalanx.

The metacarpal of the third digit is similar in length and form to that of the second digit. The proximal phalanx is slightly more than half the length of the metacarpal and almost four times the length of the more distal phalanx. On the internal surface of the digit there is an ovoid impression of keratinized tissue lying alongside the two distal phalanges.

The metacarpal of the fourth digit is the most robust of the series and



FIG. 9. Pelvic girdle, urostyle, and femur of *Eodiscoglossus santoniae* Villalta photographed under black light. Part. $\times 4.5$.

is slightly longer than the third metacarpal. Distal to the metacarpal there are three phalangeal elements that become smaller distally. The metacarpal of the fifth is somewhat robust, but smaller than the fourth, and it bears three phalangeal elements similar to those of the fourth.

PELVIC GIRDLE: The pelvic girdle (figs. 1 and 9) has been crushed flat so that the ilium is lying on its side. Its suture with the pubes can be seen clearly. The anterior arms (collum ossis ilii Bolkay) have been flattened leaving an impression of the external side. There is a clear groovelike impression indicating the existence of a thin bladelike crest on the ilium. It is not clear whether there is a distinct tuber cinereum or iliac prominence on the ilium. It is possibly present on the left side (figs. 1 and 9). Examination of the fossil under ordinary light does not seem to indicate an iliac synchondrosis, but the black light photographs do suggest this condition. The apparent contact of the bases of the ilia in the black light photographs may be due to the crushing of the pelvis. The ischium is quite well preserved and apparently had a clear crista ischii.

On the right side the arm of the ilium is preserved at its anterior tip where it makes contact with the imprint of the sacral diapophysis. On the



FIG. 10. Right tarsus and foot of *Eodiscoglossus santonjae* Villalta photographed under black light. Part. $\times 4.5$.

left side this contact of the ilium with the sacral diapophysis can be seen in the counterpart (fig. 2).

HIND LIMBS: The left femur (fig. 1) is incomplete and is represented by only the proximal portion. The head of the femur is partially exposed and appears to have been ossified. The distal portion of the bone is represented by only an imprint.

The right hind limb is almost complete. The crushed femur appears to have been ossified at both ends. It is a long columnar bone bent slightly past the midway point.

The head of the tibiofibula is rounded but crushed, and it appears to have been capped by calcified cartilage. The distal portion is similar in structure.

Distal to the tibiofibula is the incompletely preserved but well-outlined tarsal region (fig. 10). Only the proximal and distal portions of the fibulare and the tibulare are preserved as bone. It is almost certain that the two are not fused. They are both proximally and distally capped by two distinct areas, which most probably represent calcified cartilage. The tibulare is slightly shorter than the fibulare. At the distal ends of both,

which represent the proximal row of primitive tetrapod tarsalia, there is a large gap. This gap separates the two proximal bones and the row of completely preserved metatarsals. The remaining tarsalia, which were cartilaginous and not preserved, must have been in this gap. Directly posterior to the first digit the two elements of the prehallux are indicated (figs. 9 and 10). These two elements are represented on the specimen by split bone and are more evident in the photograph than in the actual material. Adjacent to the prehallux are the split elements of the first metatarsal and the first digit. The first metatarsal is expanded on either end and narrow at the waist. Distal to it lies the similarly shaped first phalanx. The distal phalanx is triangular and comes to an attenuated point.

The second digit is represented by an imprint of the second metatarsal and the split bone of the first and terminal phalanges. The first phalanx is expanded at either end, but the second is triangular in form, with an attenuated point.

The third digit is represented by an elongated metatarsal and three phalanges. The metatarsal is incompletely preserved, but the bone is split in the distal and proximal areas. The proximal phalangeal element is the longest and is similar in shape to the previously described proximal elements of the other digits. It is represented proximally and distally by split bone, and in the middle by an imprint. The first phalanx is about two-thirds the length of the metatarsal. The second distal phalanx is about two-thirds the length of the first. The distal phalanx is triangular in form and less than half the length of the more proximal phalanx.

The fourth digit is the longest. Its metatarsal is damaged on both ends but is intact in the middle. The first phalanx is about one-third shorter than the metatarsal. The second phalanx is about one-third shorter than the first, and the third is the shortest one of the series. The terminal phalanx is triangular in form.

The fifth digit is folded under the fourth, and its three distal phalanges are visible. A thin black imprint, representing the web between the digits, is evident at the level of the metacarpals of the proximal portions of the phalanges. The position of the web is probably not natural, but a result of preservation. On the median surface of the foot, at the level of the proximal tarsalia, there is an imprint of keratinized integument (fig. 10) that probably represents a secondary sexual male adornment.

PHYLOGENETIC SIGNIFICANCE

The above description of the Kimmeridgian genus *Eodiscoglossus* demonstrates that the basic osteology of the Discoglossidae was established by

the Late Jurassic. The skull and vertebral column of *Eodiscoglossus* exhibit major characters that can be used to demonstrate its affinity with living genera of this family. The presence of a plectrum distinguishes it from *Bombina*, which lacks this structure (Maree, 1945; Slabbert, 1945). The presence of a simple non-expanded sacral diapophysis in *Eodiscoglossus* indicates its similarity to *Discoglossus* and *Barbourula*. This feature, along with the absence of dermal ornamentation on the skull, distinguish it from the Tertiary *Latonia* and *Pelophilus* (Friant, 1960) and from the Cretaceous *Scotiophryne* (Estes, 1969). A unique feature of *Eodiscoglossus* may be the absence of teeth in the upper jaw. The apparent lack of rudimentary coccygeal transverse processes is remarkable. This condition may be an artifact of preservation, but as the study of Madej (1965) has demonstrated, there is great variation in this character. However, it is always present in *Bombina*.

The light-colored matrix surrounding the vertebral column (evident in the photographs) may be the remains of the calcareous secretions of the endolymphatic system (Dempster, 1930), unless it is an accident of preservation. Perhaps the unique aspect of this anuran specimen is the preservation of the keratinized integument. The presence of the nuptial pad borne on the enlarged pollex, along with secondary pads on the second and third digits, and the presence of ornamentation on the hind limb is similar to the condition found in breeding males of such genera as *Bombina* and *Discoglossus* (Knoepffler, 1961).

It may be inferred that this specimen represents a breeding male. Therefore, not only was the discoglossid morphology established by the Late Jurassic, but apparently amplexial behavior is also at least this ancient.

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